Growth and Maturity of Atlantic Cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence

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GROWTH AND MATURITY OF ATLANTIC COD (*Gadus morhua*) IN THE SOUTHERN GULF OF ST. LAWRENCE

by

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ABSTRACT

Beacham, T. D. 1983. Growth and maturity of Atlantic cod (Gadus morhua) in the southern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. 1142: iv + 31 p.

Variability in growth rates and size and age at maturity was examined for southern Gulf of St. Lawrence cod (Gadus morhua). Gillnets and long- and hand-lines caught larger cod from the same year-classes in the 1970s than did Danish seines or otter trawls. For southern Gulf of St. Lawrence cod, the mean instantaneous growth rates of ages 5 to 8 were positively correlated with water temperature, but inversely correlated with stock biomass. Instantaneous growth rates of cod were above 0.20 for age 5 or less. Median length at maturity for males declined from approximately 50 cm to 36 cm during 1959-1979, and from 60 cm to 36 cm for females during the same period. Median ages at sexual maturity declined between 2 and 3 years during the same interval. In a trend from low to high stock biomass, instantaneous growth rates of smaller cod declined more rapidly than those of larger cod, so that a year-class reached maximum biomass at age 5 under high stock biomass conditions, and about age 9 under low biomass conditions.

Key words: cod, growth, Gulf of St. Lawrence, maturity, population dynamics.

RÉSUMÉ

Beacham, T. D. 1983. Growth and maturity of Atlantic cod (Gadus morhua) in the southern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. 1142: iv + 31 p.

On a étudié, pour le sud du golfe St-Laurent, la variabilité des taux de croissance de la morue (Gadus morhua) ainsi que la taille et l'âge atteints à la maturité. De plus grosses morues provenant des mêmes classes d'âge ont été capturées, au cours des années 1970, par des filets maillants ainsi que par des palangres et des lignes à main que par des sennes danoises et des chaluts à panneaux. Pour la morue du sud du golfe St-Laurent, les taux instantanés moyens de croissance des groupes de 5 à 8 ans étaient en corrélation avec la température de l'eau, mais variaient en sens inverse de celui de la biomasse des stocks. Les taux instantanés de croissance de la morue se sont situés au-dessus de 0,20 pour les 5 ans ou moins. La longueur médiane des

mâles, à la maturité, a diminué, passant d'environ 50 cm à 36 cm entre 1959 et 1979, tandis que celle des femelles passait de 60 cm à 36 cm au cours de la même période. Pendant le même intervalle, les âges médians atteints lors de la maturité sexuelle ont diminué de 2 à 3 ans. La biomasse des stocks passant de faible à élevée, les taux instantanés de croissance des morues plus petites ont baissé plus rapidement que ceux des morues plus grosses, de sorte que la biomasse maximale a été atteinte, pour une classe d'âge, à 5 ans quand la biomasse des stocks était élevée, et à peu près à 9 ans quand celle-ci était faible.

Mots-clés: morue, croissance, golfe St-Laurent, maturité, dynamique des populations.

INTRODUCTION

The southern Gulf of St. Lawrence stock is migratory, occurring in the summer in the Gulf (Northwest Atlantic Fisheries Organization Div. 4T) and from January to April on the edge of the Laurentian Channel off the northeast coast of Cape Breton (NAFO Subdiv. 4Vn) (McKenzie 1956; McCracken 1959; Martin and Jean 1964; Kohler MS 1975) (Fig. 1). This stock supports a fishery in each area.

The cod fishery in the southern Gulf of St. Lawrence was largely a hand- and long-line fishery until the 1950s. Otter trawling began in 1947 (Paloheimo and Kohler 1968), and foreign otter trawlers began to fish this stock in Subdiv. 4Vn in the 1950s. Nominal catches from this stock peaked at about 110,000 t in 1956, at a time when herring (Clupea harengus) biomass was substantially reduced by disease (Sindermann 1958). Stock biomass generally declined through to 1975, but has recovered to levels near those of the late 1950s, owing to good recruitment of the 1973-1977 year-classes and establishment of catch quota management in 1974 (Beacham 1980).

Investigation of growth rates of the southern Gulf of St. Lawrence cod has been an area of continuing research (Kohler 1964; Paloheimo and Kohler 1968; Halliday 1972; Lett and Doubleday 1976; Lett 1978). Variability in growth rates of cod age 3 and younger in the southern Gulf of St. Lawrence has been outlined by Beacham (1981). This paper examines variability in adult growth rates because predictability of growth rates may be of prime concern for management strategy in setting future total allowable catches. Age-specific instantaneous growth rates may be analyzed to determine the age at which a year-class attains maximum biomass in order to optimize yield from a fishery. Variability in size and age at sexual maturity is the direct linkage between individual growth and reproductive potential of a population, and therefore is a parameter of concern in an investigation of population dynamics. The present paper presents some aspects of the biology of cod in the southern Gulf of St. Lawrence in relation to these problems.

MATERIALS AND METHODS

When the data from the landings of cod were analyzed on an annual basis, samples from the landings of Canadian otter trawlers, Danish seiners, long-liners, and gillnetters in Div. 4T were grouped for each fishing gear in the May through August period of each year for the period 1948-1979. However, in some years in each area, no samples were available in the four-month period under consideration. Before 1967, groundfish surveys were conducted with the M/V HARENGUS,

and details of the sampling gear are found in Powles (1965). A #36 Yankee otter trawl was used for the E.E. PRINCE surveys, which have been conducted in a stratified random design since 1970. Prior to 1970, the survey was a fixed station design, concentrated mainly in the western Gulf. Further details of the surveys were outlined by Halliday and Koeller (1981). Otoliths in the commercial and research samples were collected in a sampling design stratified by length, the design based on a method described by Gulland (1955). The age of cod was determined from otoliths as outlined by Kohler (1964). Fork lengths were measured to the nearest cm in the groundfish surveys and commercial samples. The instantaneous growth rates of cod age groups 3 to 15 were calculated from length-at-age data derived from commercially landed cod. This procedure was done separately for each fishing gear. Growth rates for each area were analyzed by analyses of covariance. Growth rate was the dependent variable, and factors of the analysis were age, sampling year, year-class, and fishing gear, with length as a covariate. Instantaneous growth rate is dependent upon body size (Parker and Larkin 1959), and thus a covariance analysis is necessary to correct for length differences among groups.

Annual values for median (50% mature point) length and age at sexual maturity of cod were derived from the September groundfish surveys. Powles (1958) outlined the classification of the gonads used in assessing maturity stage for the study. The median length at sexual maturity was calculated by probit analysis (Leslie et al. 1945) from the percentage of mature cod (gonads in ripening, ripe, spawning, spent, or recovering condition) in 2-cm length intervals in the survey or period under consideration. Median age at sexual maturity was calculated in a similar manner by grouping the data in 1-year intervals.

RESULTS

AGE AND LENGTH FREQUENCIES

An analysis of age compositions of cod in the catch of the research vessel indicated that the 1968 year-class was more abundant than the previous few, comprising about 35% of the research catch in 1972 (Fig. 2). Sizes of the 1973-1977 year-classes were generally higher than those from 1967-1972 (Beacham 1980), with the 1973 year-class comprising over 50% of the research catch in 1976. The 1975 year-class was also abundant, comprising 50% of the research catch in 1978 (Fig. 2), and the groundfish surveys have indicated that the 1975 and 1977 year-classes are the largest since surveys began in the late 1950s. About 90% of the cod caught during the surveys were age 6 or less (Fig. 3). The modal age of cod in the landings of otter trawlers in the commercial fishery declined from 8 years during the 1950s to 6 years during the 1960s and to 5 years during 1975-1979

(Fig. 4). About 60% of the cod landed during 1975-1979 were less than 54 cm in length.

GROWTH

Weights-at-age before 1970 were derived from a fixed station survey, whereas those from 1970 on were derived from a stratified random survey design. Weights-at-age have varied considerably over this interval, and there has been no unidirectional change with time (Table 1). Mean length-at-age as derived from landings in the commercial fishery have also fluctuated considerably during 1948-1979 (Fig. 5). In 1978 and 1979, weights-at-age of age 2-4 cod tend to be lower than the historical average, while those of age 10+ cod tended to be higher, having grown through a period of a general decline in stock biomass. Instantaneous growth rates were generally above 0.20 up to age 9, but there were indications that in a time of high stock biomass, such as occurred in 1979 (Beacham 1980), instantaneous growth rates were only above 0.20 up to age 5 (Table 1).

Instantaneous growth rates of cod as determined by changes in length in the May to August landings of the different gears were analyzed by analyses of covariance. Growth rates of cod were variable among years ($F=2.07$, $df=30$ and 484, $P<0.001$) and year-classes ($F=3.25$, $df=35$ and 479, $P<0.001$). The analyses also indicated that fishing gears caught cod of different mean lengths-at-age due to the different selectivities, and thus necessarily different growth rates ($F=24.86$, $df=3$ and 479, $P<0.001$).

To investigate if there were size differences between same-age cod caught in the same year by different fishing gears, I compared corresponding mean lengths over all years and all ages by sign test analysis (Mendenhall 1971, p. 369). When the mean length of cod caught by gillnets was greater than that of other gears, the comparison was scored '+'; when it was lower, it was scored '-'. This sign test analysis showed that cod of the same age caught by gillnets were larger than those caught by Danish seines (44+, 2-, $P<0.01$) and otter trawls (63+, 2-, $P<0.01$) in the same year, but not significantly larger than those caught by long- and hand-lines (23+, 12-, $P>0.20$). Similarly, same-age cod caught by long- and hand-lines were larger than same-age cod caught by Danish seines (29+, 7-, $P<0.01$) and otter trawls (60+, 17-, $P<0.01$). There was no difference between mean lengths of cod caught by Danish seines and otter trawls (51+, 34-, $P<0.20$). Thus, gillnets and long- and hand-lines selected the larger members of a year-class as compared with Danish seines and otter trawls.

To examine if growth rates of cod were dependent upon population biomass, numbers and water temperature, I determined instantaneous growth rates of ages 5 through 8 and population biomass of ages 3+ from 1958 through 1978. Before 1958, growth rates of cod were confounded by an epizootic that occurred in the mid-1950s in the

herring populations. Biomass was determined by using the weights-at-age from Table 1, numbers-at-age in the stock from 1960 through 1978 from Beacham (1980), and numbers-at-age from 1958-1959 from Lett (1978).

Instantaneous growth rates of age 5 cod were inversely related with age 3+ biomass ($r=-0.50$; $n=20$; $P<0.05$), as were growth rates of age 6 cod ($r=-0.47$; $n=19$; $P<0.05$), age 7 cod ($r=-0.46$, $n=19$, $P<0.05$), but the relationship was not statistically significant for age 8 cod ($r=-0.23$; $n=20$; $P>0.10$). Growth rates of age 5 cod were inversely related with age 3+ numbers ($r=-0.48$; $n=20$; $P<0.05$), as were growth rates of age 6 cod ($r=-0.39$; $n=19$; $P<0.10$), age 7 cod ($r=-0.51$; $n=19$; $P<0.05$), but the relationship was not significant for age 8 cod ($r=-0.13$; $n=20$; $P>0.10$). Thus instantaneous growth rates of ages 5 through 7 cod were inversely related with both biomass and numbers.

To determine if growth rates of cod ages 5 through 8 were influenced by water temperature, I examined the relationship between growth rates and the mean surface temperature recorded from May through August at Entry Island in the Magdalen Islands (61°40'W, 47°15'N). However, it is necessary to determine the partial correlation between growth rates and water temperature in order to correct for biomass effects. Between 1958 and 1978, the arithmetic mean of instantaneous growth rates of ages 5 through 8 were related to water temperature (partial $r=0.42$; $n=20$; $P<0.10$), with higher growth rates occurring at higher water temperatures (Table 2).

A method to predict future growth rate changes was investigated because changes in weights-at-age can have a significant impact on projected total allowable catches. Multiple regression was used to determine the effects of weight, population biomass, and their interactions on instantaneous growth rate as determined by changes in weight with age. The model was fitted by investigating changes in age specific instantaneous growth rates of ages 3-9 that were derived by sampling the landings of otter trawlers from May through August from 1958-1978. Instantaneous growth rates greater than 0.45 for age 5, 0.35 for age 6, 0.30 for ages 7-9, and negative rates were considered an artifact of poor sampling and biologically unrealistic, and were therefore excluded from the analysis. The model fitted was

$$G = b_1W + b_2W^2 + b_3\ln B + b_4\ln W \times B + K$$

where G = age-specific instantaneous growth rate in one year
W = weight in kg for each age
B = biomass of cod stock in metric tonnes
K = regression constant

The analysis yielded:

Variable	Coefficient	SE	t
W	0.784	0.156	5.02
W^2	-0.094	0.023	-4.12
ln B	0.689	0.117	5.90
ln W×B	-0.810	0.107	-7.60
K	1.091		

The multiple correlation was 0.88 (R^2=0.77) (Table 3), with the regression being highly significant (F=68.13, df=4, 98, P<0.01). The variable that accounted for the greatest amount of the variability in instantaneous growth rate was the interaction between stock biomass and weight of a fish.

SEXUAL MATURITY

Maturity stock biomass was high in the late 1950s following a period of high growth rates and good recruitment in the mid-1950s, concurrent with a decline in herring (Clupea harengus) biomass following an epizootic disease (Sindermann 1958). Median length at sexual maturity has generally declined from 46 cm for males and 56 cm for females in 1959 to about 36 cm for both males and females in 1979 (Fig. 6). For female cod, median length at sexual maturity decreased by about 36%, and for males, about 22%. Females usually matured at larger lengths than did males. Median age at sexual maturity show trends similar to those of length (Fig. 7). Median age at sexual maturity has declined about 50% for female cod and about 30% for male cod. Males matured younger than did females. However, the difference in median size and age at maturity between males and females was greater in the late 1950s and early 1960s than in the 1970s. Confidence limits for median size and age at maturity were generally wider in the earlier years in the analysis than in the later because sample sizes were smaller in the earlier years.

Maturity ogives based on length and age were calculated for four periods in this study, each roughly corresponding to a five-yr interval. The transition from the immature to the mature state followed a sigmoid curve (Fig. 8). Median lengths at maturity for cod in 1959-1964 were 45.5 cm for males and 54 cm for females, but in 1975-1979 these values were 39 cm and 40 cm respectively, and these values were lower than in any of the three previous intervals (P<0.01). There has been a shift towards smaller lengths at both the upper and lower end of the maturity ogives, with the shift more pronounced at the upper end. By 1975-1979, immature cod over 50 cm in length had largely disappeared from the stock, but during 1959-1964, about 30% of the males and 60% of the females over 50 cm in length were immature. For female cod, the transition from 0% mature to 100%

mature occurred over a 40-cm interval in 1959-1964, but the transition occurred over a 20-cm interval in 1975-1979. Larger, immature cod became progressively less abundant in the stock.

Changes in percent mature by age indicate that there has been an increase in percent mature at each age through time (Table 4). During 1959-1964, median age at maturity was 5.0 yr for males and 6.1 yr for females, but during 1975-1979, median age at maturity was 3.6 yr for both sexes, the difference between periods being statistically significant ($P<0.01$). For males, there has been a marked increase in percent mature for ages 3-5 over time (Table 4). The trend has been even more striking for females ages 3-6. There were 17% of age-5 females mature in 1959-1964, but about 96% mature from 1975-1979. In 1975-1979, virtually all cod age 5 and older were sexually mature. Variability in percent mature by age for females was also investigated by year-class. The percent mature at age 5 increased from 0% in the 1955 year-class to 97% in the 1974 year-class (Table 5). In 1974, 26% of the females in the 1970 year-class were mature, but by 1975 about 96% were mature. Similarly, in 1974, 13% of the females in the 1971 year-class were mature, but about 74% were mature in 1975. Thus there was a rapid increase in percent mature by age in 1975 as compared with 1974.

DISCUSSION

Temperature and growth rate in cod have been linked in some stocks (Hermann and Hansen 1965; Jonsson 1965; May et al. 1965; Wiles and May 1968; Pinhorn 1969; Ponomarenko 1973), with higher growth rates generally found at higher water temperatures. However, slower growth rates may not be necessarily indicative of lower water temperatures. Brett et al. (1969) showed that for sockeye salmon (Oncorhynchus nerka), the optimum temperature for growth was dependent upon the ration available, with fish growing faster at lower temperatures if less than the maximum ration was provided. Stock density has been suggested to have a significant impact on growth rates (Kohler 1964; Paloheimo and Kohler 1968; Lett and Doubleday 1976; Lett 1978). This study supported the hypothesis of an effect of water temperature on growth rates, and suggests an effect of stock biomass, with growth rates declining as stock biomass increased. Competition for food may be the mechanism of this density-dependence, as unusually high growth rates were recorded from 1954-1956, a time of declining herring fish biomass due to disease (Sindermann 1958), and the increased availability of herring as food (Kohler 1964).

Variability in growth rates of some fish stocks may be attributable to changes in gene frequencies for genes controlling growth. Growth rates of rainbow trout (Salmo gairdneri) can be influenced by selection (Kincaid et al. 1977). The selective removal of fast-growing individuals by fishing has been suggested to account

for the decrease in size with time of pink salmon (Oncorhynchus gorbuscha) (Ricker et al. 1978) and brown trout (Salmo trutta) (Favro et al. 1979). For southern Gulf of St. Lawrence cod, there has been no general decline in weight with time, which suggests that either the fishery has not been selectively removing fast-growing individuals or that environmental rather than genetic changes have more influence on cod growth rates.

The present study has indicated that there is an interaction between population biomass and weight of a fish when changes in instantaneous growth rates were examined. Lighter cod experienced more of a decline in growth rates at high population biomass than did heavier cod, similar to the conditions noted by Paloheimo and Kohler (1968), Lett et al. (1975), and Lett (1978). This result suggests that at high population biomass, intraspecific competition becomes more pronounced, and that the smaller cod are less able to compete with larger cod for resources, presumably food.

The depression of growth rates of smaller cod at higher stock biomasses suggests that different fishing strategies should be employed for low and high stock biomass conditions. If natural mortality is 0.20, then under lower stock biomasses, a year-class reaches maximum biomass at about age 9, but under high biomass conditions such as occurred in this stock in the late 1950s, maximum biomass of a year-class is attained at about age 5. If management strategy is to obtain maximum yield of a year-class, then under high stock biomass conditions, younger fish should constitute a higher proportion of the catch than under low stock biomass conditions.

Median length and age at sexual maturity for cod in the Gulf of St. Lawrence has been an area of some research. Variability in median length at sexual maturity for Div. 4T cod was investigated by Powles (1958), who found that during the summers of 1955 and 1956, median lengths at maturity for females were between 52 and 57 cm, and those for males between 50 and 53 cm. The present study indicates that median lengths at maturity for cod in Div. 4T between 1959-62 were similar to those recorded by Powles (1958), but that they subsequently declined, as noted by Lett (1978). Wiles and May (1968) found that, by grouping data between 1947-1966, the median lengths at sexual maturity in the northern Gulf of St. Lawrence cod stock (Divs. 3Pn-4RS) were 46 cm for males and 50 cm for females, corresponding to median ages at maturity of 5.1 yr and 6.1 yr respectively. Minet (1978), investigating the same stock in 1973, found results very similar to those of Wiles and May (1968). Pinhorn (1969) found similar results for cod in Subdiv. 3Pn in 1952, but median ages apparently increased to 6.3 yr for males and 6.7 yr for females in 1957. Fleming (1960) found that cod in the same area matured between 6.6 and 6.8 yr from 1947-1950. Thus it appears for the northern Gulf of St. Lawrence cod stock, there has not been a marked decline in median age at sexual maturity with time. In Div. 4T cod, stock biomass was at a minimum in 1975, and there was a rapid increase in percent mature by age in 1975 as compared with 1974, which suggests that age at maturity was responding to changes in stock biomass.

In summary, cod of the same age were larger in gillnet and long- and hand-line landings than in Danish seine and otter trawl landings. Variability in growth rates of the southern Gulf of St. Lawrence cod stock was positively related to changes in water temperature, and inversely related to stock biomass. As stock biomass increased, growth rates of smaller cod declined more than did those of larger cod. Size and age at sexual maturity declined during a period of heavy exploration of the stock and remained low after stock biomass started to recover. Investigations as to whether growth rates are dependent upon stock biomass ought to be conducted for other species and stocks. These results should be incorporated into fishery assessment models for providing advice on total allowable catches.

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Table 1. Mean weight-at-age (kg) for cod caught during September cruises in Div. 4T of the research vessels HARENGUS and E.E. PRINCE. Number of otoliths read for each age is in parentheses.

Age	1959	1960	1961 *	1963	1964	1965	1966	1967	1968	1969
2	0.14(19)	0.17(38)	0.15(36)	0.19(136)	0.19(68)	0.22(35)	0.17(69)	0.20(51)	0.19(61)	0.18(42)
3	0.36(33)	0.34(117)	0.30(45)	0.37(72)	0.39(160)	0.40(86)	0.37(89)	0.44(128)	0.42(126)	0.43(77)
4	0.65(49)	0.66(136)	0.55(102)	0.60(83)	0.57(95)	0.68(89)	0.78(86)	0.70(117)	0.81(185)	0.84(89)
5	1.24(84)	1.10(73)	0.89(102)	0.91(57)	0.90(130)	1.18(34)	1.28(75)	1.45(90)	1.36(138)	1.41(106)
6	1.61(80)	1.73(72)	1.35(58)	1.08(145)	1.19(76)	1.23(59)	1.59(38)	1.89(89)	1.91(89)	2.03(29)
7	2.00(64)	2.00(19)	2.07(36)	1.46(138)	1.35(143)	1.67(27)	1.91(41)	2.40(39)	2.62(86)	2.77(32)
8	2.81(40)	2.76(15)	2.76(24)	2.01(40)	1.96(95)	2.02(58)	2.27(16)	2.48(22)	3.64(37)	3.71(25)
9	3.49(80)	3.69(6)	3.63(12)	2.83(25)	2.58(33)	2.54(52)	2.45(43)	2.90(13)	2.56(29)	4.83(8)
10	3.74(29)	3.18(7)	5.23(4)	5.02(14)	4.38(25)	2.92(17)	3.41(30)	4.22(20)	2.94(9)	2.94(12)
11	5.17(21)	3.68(6)	6.89(7)	3.03(5)	6.91(9)	5.05(5)	4.86(22)	4.72(16)	3.96(16)	9.70(1)
12	5.75(15)	4.20(3)	7.23(5)	8.42(4)	9.30(3)	- (0)	6.71(22)	6.34(11)	5.31(18)	5.43(12)
13	10.01(7)	4.37(2)	7.77(5)	9.35(2)	- (0)	8.59(4)	8.07(11)	8.25(2)	6.27(6)	7.68(5)
14	7.98(3)	13.37(1)	8.98(3)	6.14(1)	4.63(2)	- (0)	10.31(4)	10.57(4)	9.53(8)	9.68(3)
15	- (0)	6.14(1)	15.50(1)	- (0)	- (0)	9.70(1)	- (0)	11.60(3)	10.78(2)	10.74(2)

Table I (cont'd)

Age	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
2	0.18(94)	0.13(34)	0.15(83)	0.17(149)	0.21(102)	0.09(171)	0.16(128)	0.13(234)	0.17(110)	0.11(169)
3	0.42(197)	0.42(226)	0.39(134)	0.33(222)	0.46(286)	0.29(177)	0.27(390)	0.33(343)	0.33(406)	0.25(216)
4	0.78(186)	0.75(202)	0.73(335)	0.75(144)	0.74(225)	0.74(244)	0.72(245)	0.66(366)	0.71(429)	0.59(337)
5	1.20(237)	1.16(202)	1.22(171)	1.20(227)	1.18(112)	1.20(218)	1.31(178)	1.40(214)	1.21(281)	0.97(342)
6	1.77(275)	1.43(177)	1.56(174)	1.56(123)	1.69(147)	1.79(88)	1.92(97)	1.90(332)	2.14(100)	1.48(260)
7	2.55(104)	1.96(149)	1.95(140)	1.93(103)	2.15(66)	2.36(67)	2.50(36)	2.71(79)	2.60(62)	2.17(100)
8	3.35(48)	3.01(50)	2.73(100)	2.38(88)	2.33(49)	2.85(47)	3.15(28)	4.42(42)	3.54(23)	2.77(50)
9	4.12(43)	4.24(14)	3.98(23)	2.83(63)	2.49(46)	3.29(22)	3.16(13)	4.03(29)	5.39(7)	3.64(26)
10	4.15(9)	5.66(16)	5.01(18)	5.00(18)	3.64(20)	4.25(15)	4.18(15)	5.54(22)	7.18(12)	6.86(10)
11	3.76(14)	5.57(8)	6.69(18)	3.74(5)	5.20(8)	4.67(18)	5.52(14)	5.04(18)	6.54(6)	7.37(10)
12	4.16(11)	3.92(5)	7.68(8)	7.94(9)	5.99(6)	5.69(5)	4.93(5)	5.49(16)	7.60(3)	6.41(5)
13	4.42(12)	3.53(1)	5.55(3)	3.61(2)	10.44(6)	10.61(3)	6.91(2)	6.28(12)	- (0)	11.40(3)
14	7.26(9)	4.85(5)	9.80(2)	3.14(4)	- (0)	11.81(1)	4.89(1)	- (0)	7.55(4)	5.65(2)
15	7.15(2)	6.35(7)	6.13(2)	4.89(1)	4.31(1)	13.92(1)	3.39(1)	14.94(3)	10.65(2)	13.85(2)

*There were insufficient otoliths collected in the September 1962 survey to provide mean weights-at-age for that year.

Table 2. Arithmetic means of instantaneous growth rates with respect to length of cod ages 5 to 8 caught in the Gulf of St. Lawrence.

Year	Entry Island temperature (°C)	4T
1958	12.2	0.043
1959	11.8	0.091
1960	13.8	0.077
1961	10.4	0.050
1962	10.7	0.049
1963	11.2	0.069
1964	11.2	0.083
1965	11.7	0.121
1966	12.4	0.106
1967	11.8	0.087
1968	12.5	0.138
1969	12.1	0.072
1970	13.1	0.102
1971	12.5	0.052
1972	11.0	0.085
1973	11.6	0.105
1974	11.7	0.137
1975	11.6	0.107
1976	12.1	0.093
1977	9.1	0.059

Table 3. Correlation matrix of the cod growth model. Variables are listed in the text.

Variables	G	W	W2	ln B	ln B×W
G	1.00	-0.61	-0.50	-0.44	-0.80
W		1.00	0.95	0.17	0.61
W^2			1.00	0.15	0.74
ln B				1.00	0.61
ln B×W					1.00

Table 4. Percentages of sexually mature cod by age and sex caught during Canadian groundfish surveys in the southern Gulf of St. Lawrence 1959-1979. Sample sizes are in parenthesis after individual ages and 95% confidence limits after A_{50} (yr).

Age (yr)	1959-1964	1965-1969	1970-1974	1975-1979
		Male		
2	0.0 (316)	0.0 (216)	3.0 (264)	0.7 (542)
3	1.7 (482)	1.5 (392)	10.5 (631)	15.4 (1204)
4	17.6 (501)	30.0 (537)	42.6 (775)	68.6 (1184)
5	53.9 (623)	67.6 (395)	84.9 (657)	95.8 (866)
6	78.4 (570)	89.2 (251)	97.6 (579)	99.3 (457)
7	91.4 (452)	97.1 (207)	98.5 (343)	100.0 (247)
8	95.7 (230)	99.1 (106)	100.0 (228)	100.0 (134)
9	99.5 (205)	97.9 (95)	100.0 (123)	98.6 (72)
10	99.0 (110)	98.4 (62)	97.3 (37)	100.0 (51)
11	98.4 (62)	100.0 (60)	100.0 (24)	100.0 (43)
12	100.0 (36)	100.0 (52)	100.0 (18)	100.0 (29)
A_{50}	4.96(4.89-5.04)	4.55(4.48-4.63)	4.01(3.96-4.07)	3.58(3.54-3.62)
		Female		
2	0.0 (257)	0.0 (172)	0.4 (255)	2.4 (542)
3	0.2 (481)	2.2 (367)	4.0 (607)	19.4 (1164)
4	2.3 (473)	23.7 (485)	25.3 (704)	62.7 (1209)
5	17.3 (595)	66.6 (332)	68.9 (592)	95.6 (882)
6	50.8 (563)	89.2 (223)	90.0 (571)	99.1 (458)
7	74.4 (460)	98.4 (187)	98.6 (356)	98.1 (209)
8	87.7 (236)	100.0 (126)	100.0 (189)	99.1 (113)
9	96.8 (216)	99.0 (103)	100.0 (96)	100.0 (51)
10	98.4 (122)	98.2 (55)	100.0 (54)	100.0 (51)
11	98.7 (76)	100.0 (51)	100.0 (35)	100.0 (44)
12	95.8 (48)	97.3 (37)	100.0 (24)	100.0 (17)
13	95.7 (23)	100.0 (13)	100.0 (6)	100.0 (4)
14	100.0 (17)	100.0 (7)	100.0 (12)	100.0 (6)
A_{50}	6.08(5.99-6.17)	4.62(4.55-4.70)	4.53(4.48-4.59)	3.60(3.56-3.64)

Table 5. Percent of female cod classified as mature during autumn groundfish surveys in the southern Gulf of St. Lawrence for the 1955-1977 year-classes.

Year-class	Age (yr)								
	1	2	3	4	5	6	7	8	9
1955				0.0 (22)	0.0 (18)	12.5 (24)	96.2(26)	100.0(19)	94.1(17)
1956			0.0 (16)	0.0 (24)	5.3 (38)	70.3 (37)	81.1(74)	84.0(50)	100.0(27)
1957		0.0 (11)	0.0 (6)	0.0 (31)	36.7 (49)	52.2 (69)	62.1(58)	100.0(39)	100.0(18)
1958	0.0 (1)	0.0 (1)	0.0 (13)	3.6 (28)	30.8 (26)	48.7 (39)	100.0(14)	100.0(25)	100.0 (6)
1959	0.0 (1)	0.0 (15)	3.1 (32)	7.5 (40)	15.1 (53)	93.9 (33)	100.0(16)	100.0(13)	100.0 (9)
1960	0.0 (1)	0.0 (15)	0.0 (39)	0.0 (58)	69.2 (13)	83.7 (43)	94.1(17)	100.0(13)	100.0 (7)
1961	0.0(20)	0.0 (62)	0.0 (76)	18.9 (37)	57.1 (21)	79.0 (38)	100.0(39)	100.0(22)	100.0 (7)
1962	0.0 (2)	0.0 (26)	2.4 (42)	7.5 (40)	50.0 (48)	88.0 (25)	100.0(18)	100.0(22)	100.0 (7)
1963	0.0 (4)	0.0 (18)	1.3 (59)	9.6 (52)	58.3 (60)	100.0 (18)	98.0(50)	100.0(21)	100.0 (9)
1964	0.0 (6)	0.0 (16)	1.6 (61)	10.0 (80)	59.6 (52)	82.9(117)	97.0(67)	100.0(39)	100.0(27)
1965	0.0 (4)	0.0 (15)	0.0 (60)	8.5 (47)	46.3(108)	87.5 (88)	100.0(74)	100.0(46)	100.0(17)
1966	0.0 (1)	0.0 (30)	0.0 (46)	2.3 (89)	57.7 (97)	91.7 (86)	100.0(52)	100.0(23)	100.0 (8)
1967	0.0 (3)	0.0 (27)	0.0(102)	13.9(101)	69.3 (88)	98.5 (67)	94.6(37)	100.0(20)	100.0 (6)
1968	0.0 (3)	0.0 (47)	0.0(116)	29.8(151)	93.7 (95)	91.1 (79)	97.1(35)	100.0 (8)	100.0 (9)
1969	0.0 (1)	0.0 (14)	1.5 (67)	48.4 (64)	66.0 (53)	100.0 (38)	100.0(16)	100.0(18)	100.0 (2)
1970	0.0 (2)	0.0 (45)	4.6(110)	25.9(116)	95.6(113)	100.0 (52)	100.0(30)	100.0(14)	100.0(18)
1971	0.0 (6)	0.0 (80)	12.5(120)	74.1(116)	96.4 (83)	98.1 (53)	100.0(27)	96.8(31)	
1972	0.0 (2)	2.4 (42)	11.1 (90)	51.2(123)	90.2(112)	100.0 (47)	94.8(58)		
1973	0.0 (2)	1.4 (72)	3.3(183)	28.1(171)	96.0(149)	98.2(169)			
1974	0.0 (2)	0.0 (69)	1.7(176)	78.2(229)	97.4(193)				
1975	0.0(32)	0.0(122)	39.9(198)	64.2(218)					
1976	0.0(12)	7.4 (54)	31.6(136)						
1977	0.0(13)	3.9(102)							

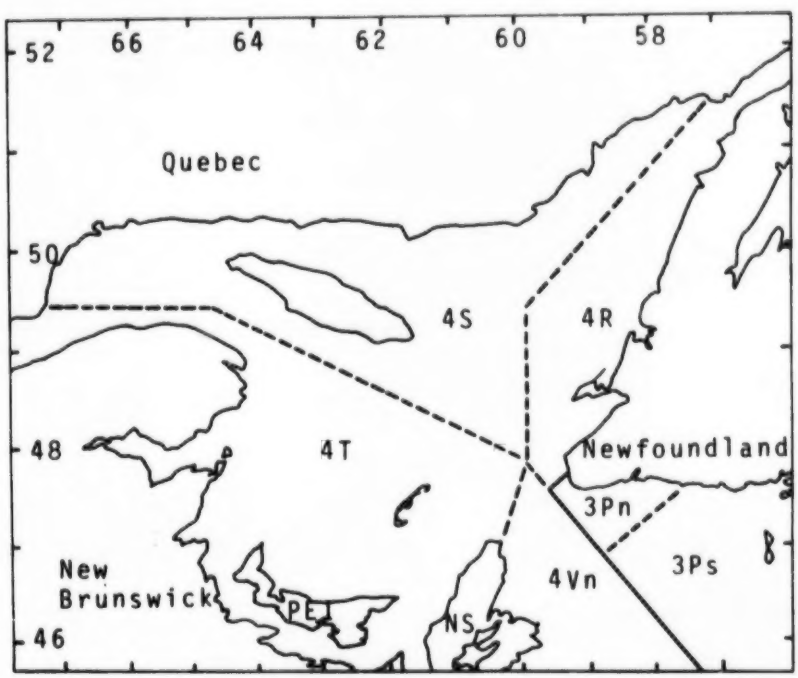

Fig. 1. NAFO Divisions and Subdivisions in the Gulf of St. Lawrence.

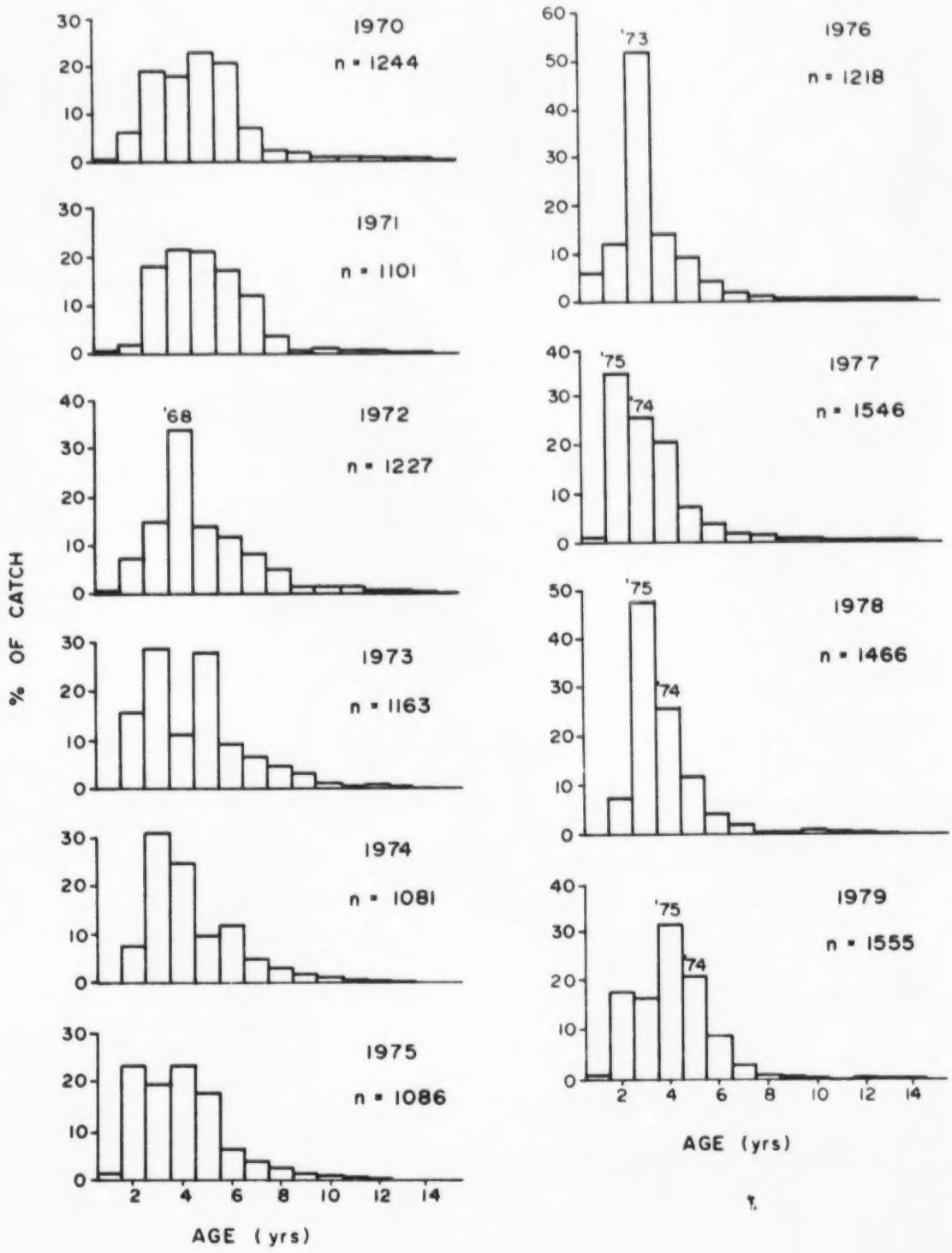

Fig. 2. Annual age compositions of cod caught during September groundfish cruises in Div. 4T, 1970-1979.

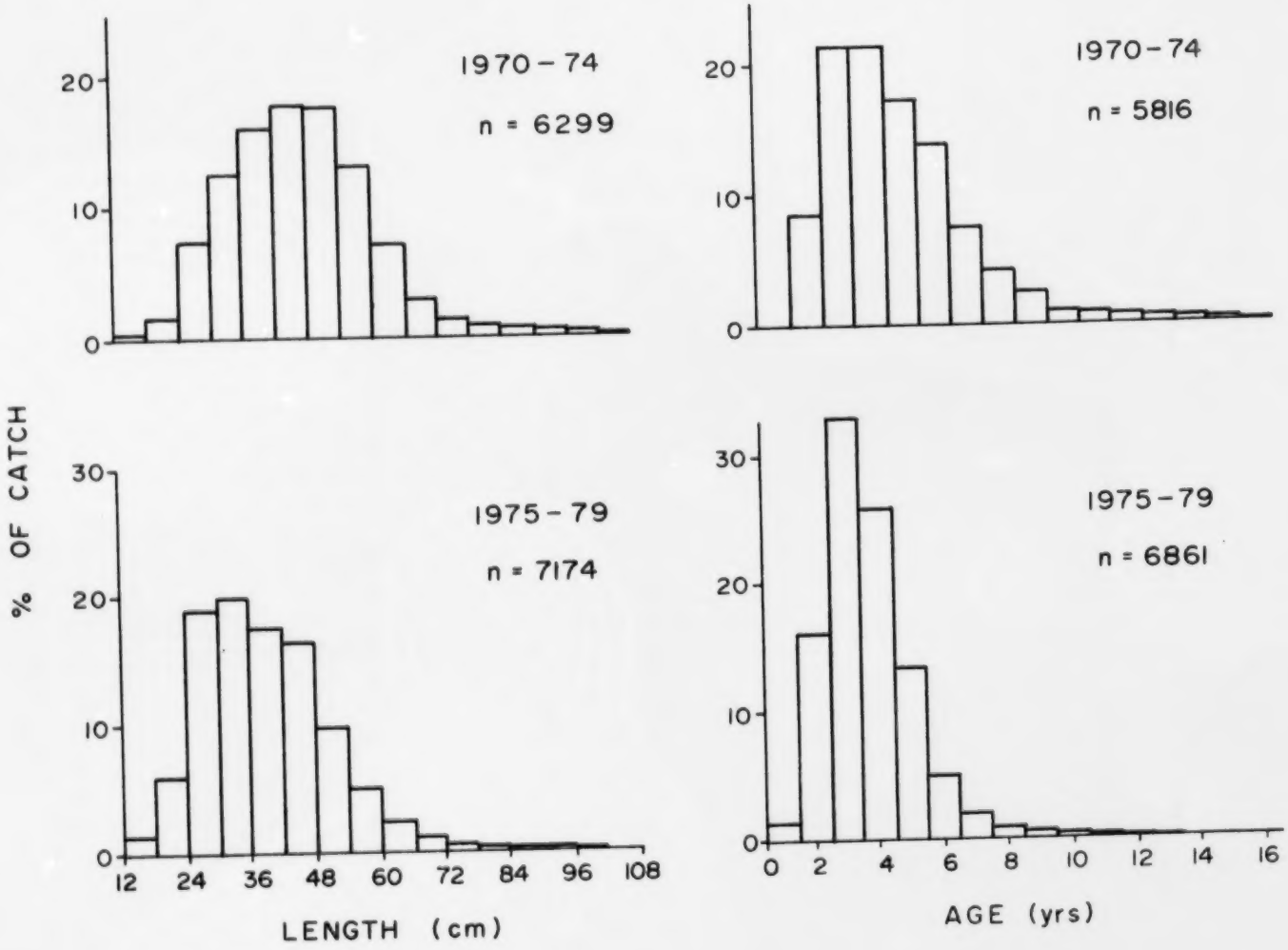

Fig. 3. Length frequencies and age compositions of cod caught during September groundfish surveys in the southern Gulf of St. Lawrence, 1970-1974 and 1975-1979.

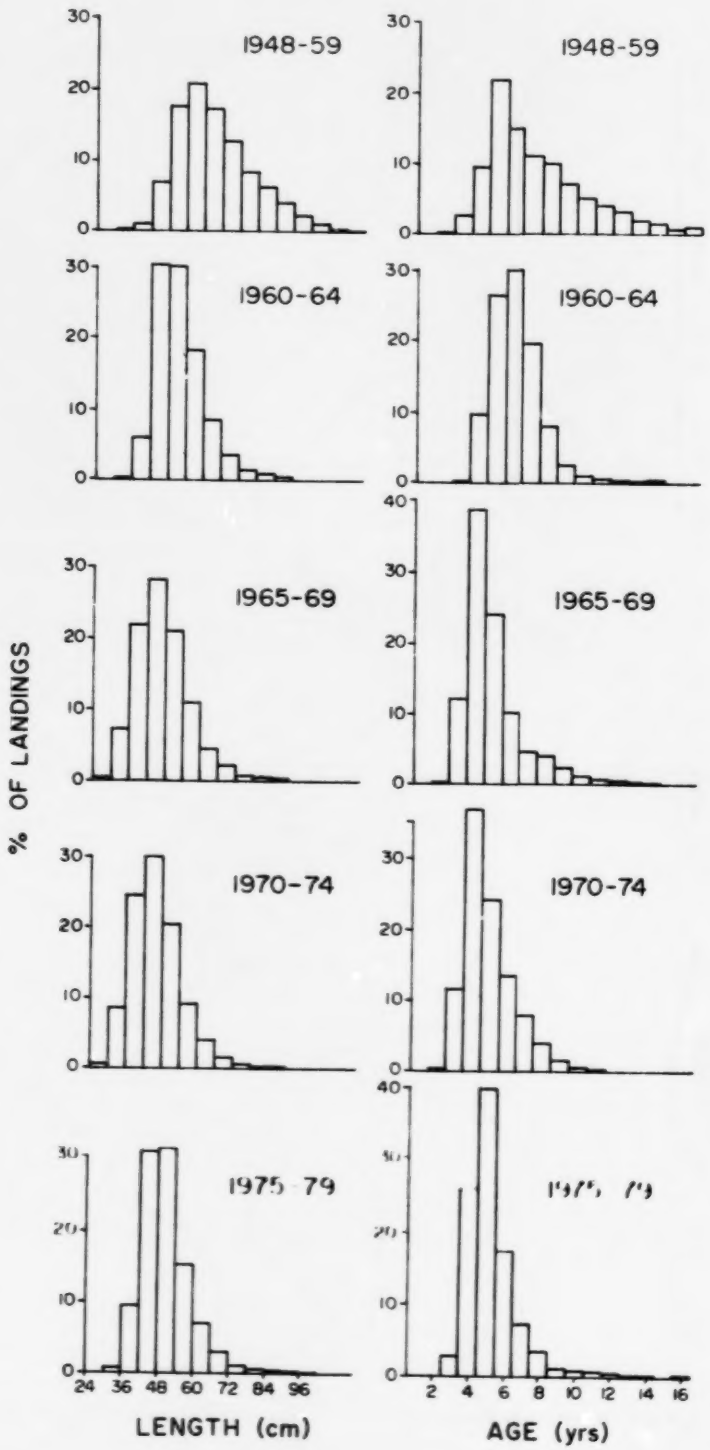

Fig. 4. Length frequencies and age compositions of cod in the May through August landings of Canadian otter trawlers in the southern Gulf of St. Lawrence, 1948-1979.

Fig. 5. Mean length-at-age of cod in the May to August landings in the southern Gulf of St. Lawrence, 1948-1979.

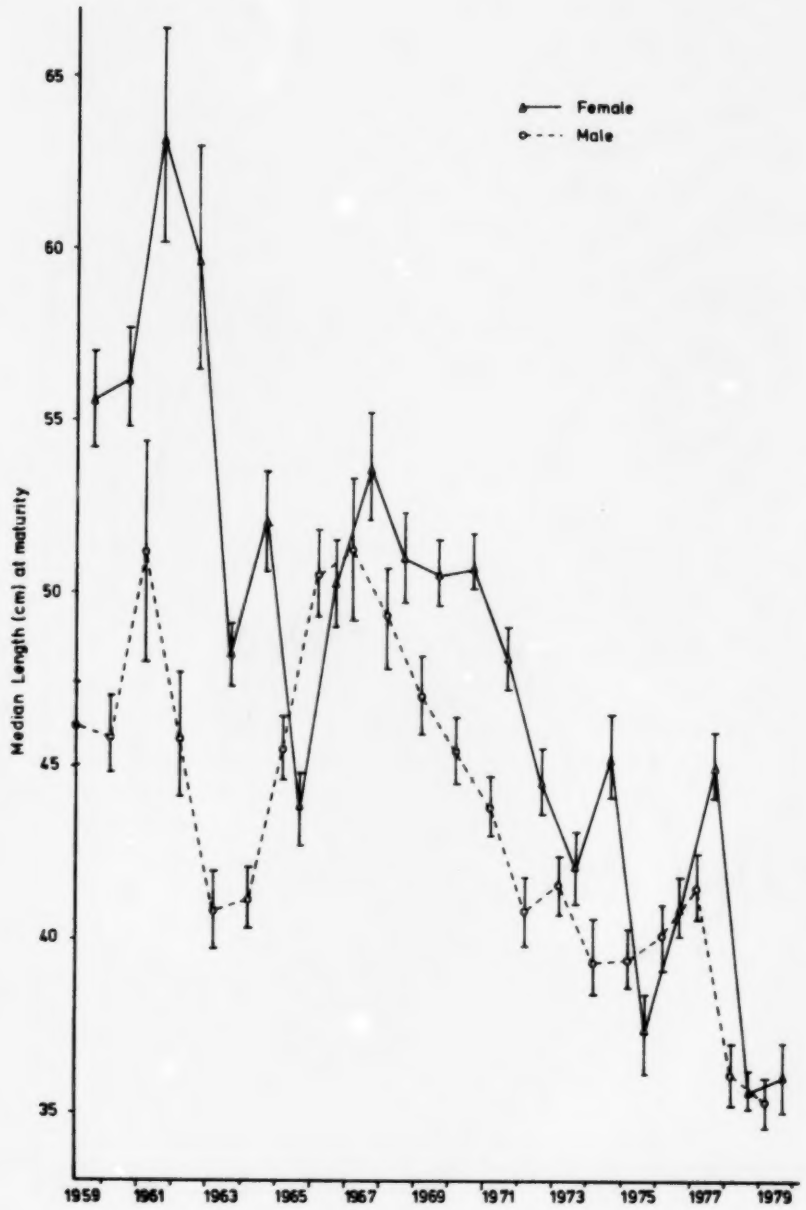

Fig. 6. Median length at sexual maturity for cod sampled during autumn groundfish surveys in Div. 4T, 1959-1979. Vertical bars indicate 95% confidence limits.

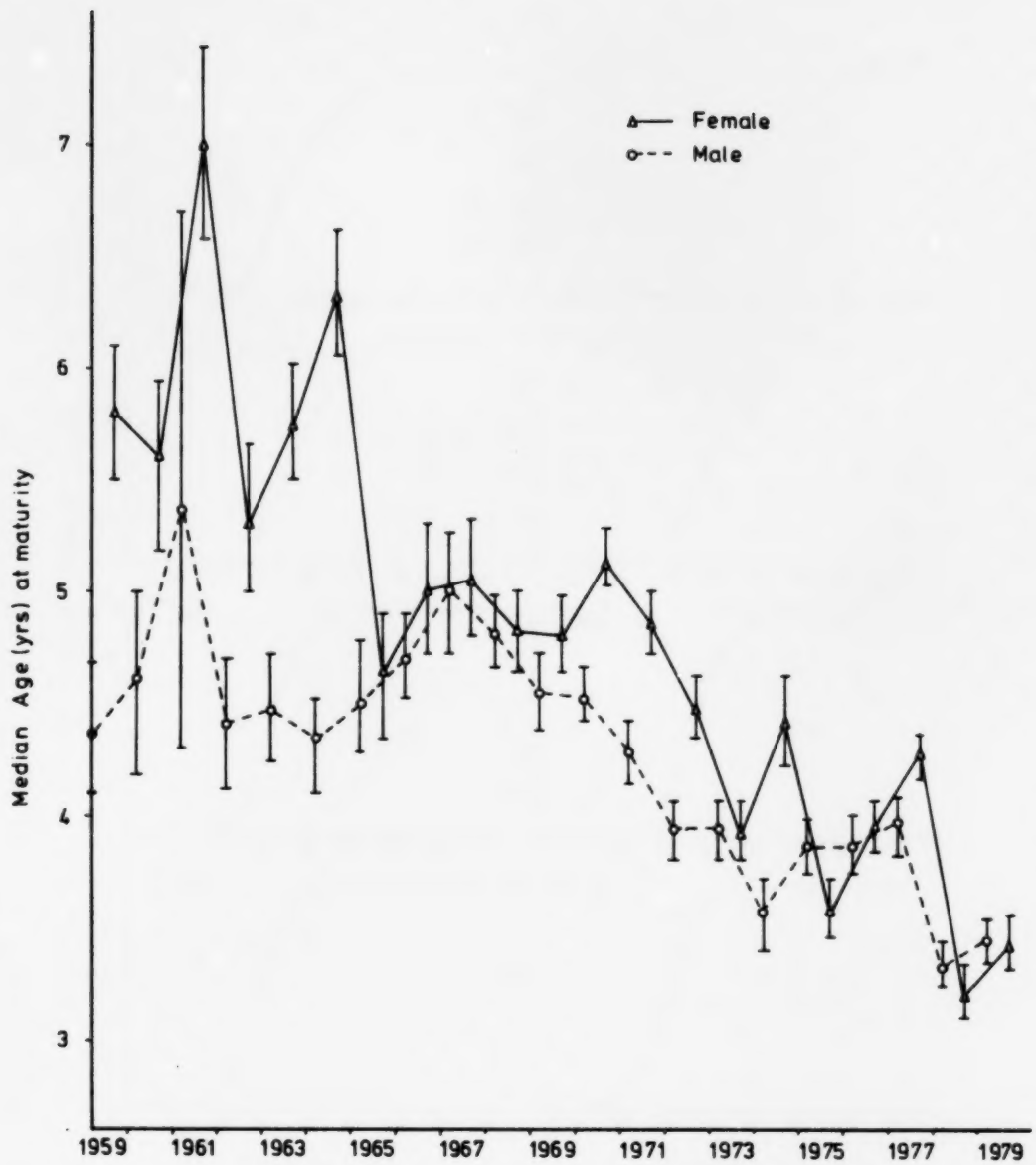

Fig. 7. Median age at sexual maturity for cod sampled during autumn groundfish surveys in Div. 4T, 1959-1979. Vertical bars indicate 95% confidence limits.

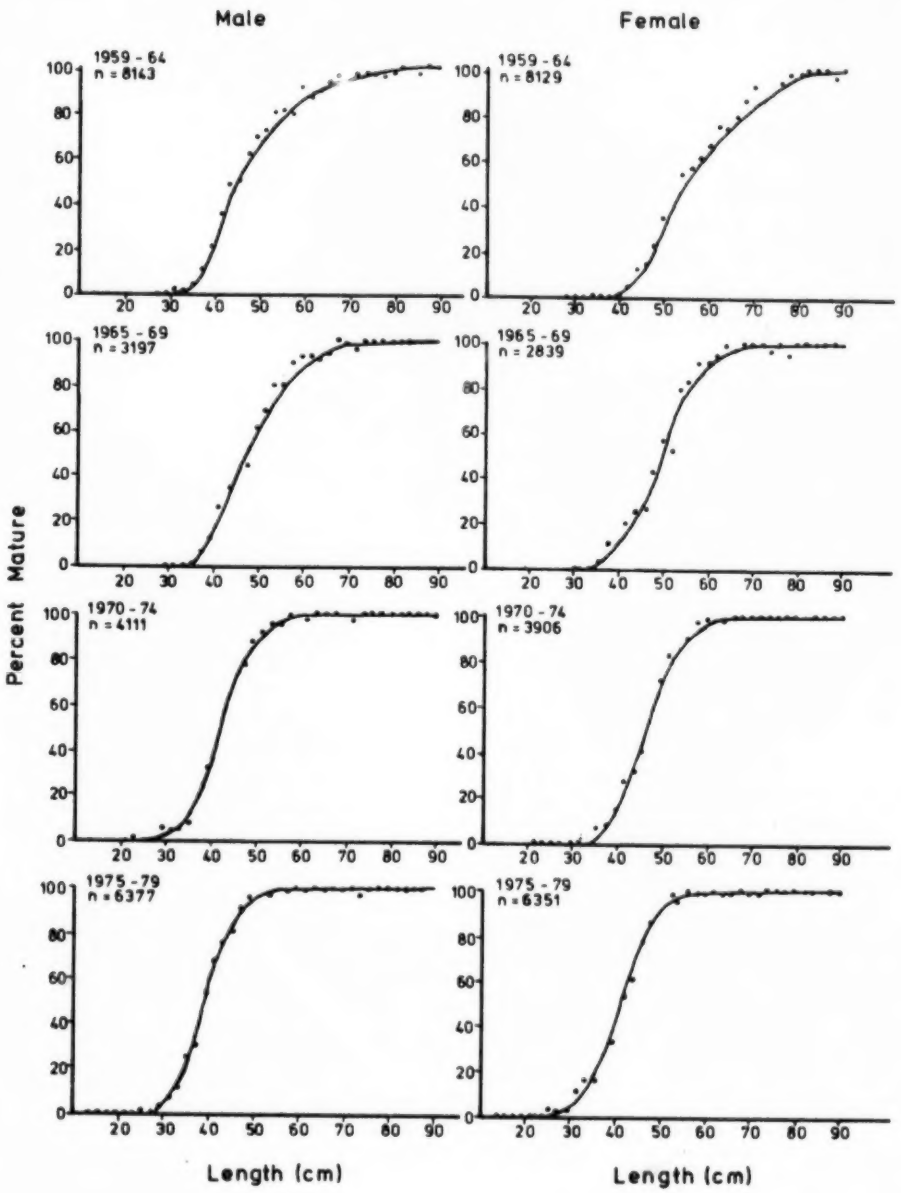

Fig. 8. Maturity ogives for cod caught during Canadian groundfish surveys in Div. 4T, 1959-1979.